

昆虫聚集信息素

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摘要: 昆虫聚集信息素是昆虫重要的信息化学物质之一, 对昆虫的聚集行为有重要意义。近三十年来, 国外鉴定了多种昆虫聚集信息素, 主要成分为一些烃、醇、醛、酮、酯、酸、酸酐、胺以及腈类化合物, 但其在有害生物可持续治理中的应用潜能尚未充分利用; 昆虫聚集信息素的来源多样, 除蛹外, 多个虫态均有聚集信息素释放, 有些学者甚至把一些寄主释放的挥发物作为聚集信息素的组分; 同种昆虫, 不同生理状态, 其聚集信息素可以完全不同或同一信息化学物质的功能不同; 但是, 并非所有昆虫的聚集行为均为聚集信息素调节, 利他素、性信息素以及报警信息素等其它信息化学物质均能导致一些昆虫的聚集。本文综述了 5 目 17 科 55 种昆虫的聚集信息素。

关键词: 昆虫; 聚集; 信息素

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The aggregation pheromones of insects

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Abstract: Aggregation pheromones are important semiochemicals in insects that play a key role in mating and other social behavior. Many chemicals, including hydrocarbons, alcohols, aldehydes, ketones, esters, acids, anhydrides, amines, and nitriles, have been identified as insect aggregation pheromones, however, understanding of their potential utility in pest management is still limited. Aggregation pheromones have been found in eggs, larvae and adults, however, some volatiles from host plants have been regarded as pheromone components. Aggregation pheromones of the same species in different stages of the life-cycle can be distinct, and the same semiochemical may induce different behavior in different developmental stages or physical states. Nevertheless, the aggregation of insects can be regulated by semiochemicals such as kairomone, sex pheromone and alarm pheromone. Understanding of insect aggregation pheromones is still inadequate and determining the precise function of these chemicals requires further research.

Key words: insects; aggregation; pheromone

昆虫能在充满竞争的环境中生存, 是因为它们已经发展了惊人的适应性或能力, 能通过视觉信号、听觉信号以及嗅觉(化学)信号来获取信息, 从而完成寻找资源和躲避灾难等活动。昆虫在整个生命周期中的许多行为活动受信息化学物质调节和控制, 许多昆虫必须依靠它们对气味的感觉才能而生存。二十多年来, 国内外发展利用昆虫本身生理生化特性和行为特点作为害虫可持续治理的一种新技术日益受到重视, 其中, 昆虫信息素的研究利用

尤为突出(杜家纬, 1988, 1991; 刘孟英, 1994)。

昆虫信息素对昆虫的定向、召唤、交尾、产卵、聚集、追踪、告警、防御以及种间识别等行为均具有重要的作用。昆虫聚集信息素(aggregation pheromone)通常被定义为由昆虫产生, 并能引起雌、雄两性同种昆虫聚集行为反应的化学物质。昆虫通过聚集或获得有益的环境, 或共享资源, 或抵御外敌的侵袭。

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1 昆虫聚集信息素的成分

最早分离、鉴定并合成的昆虫聚集信息素是森林害虫异加州齿小蠹 *Ips paraconfusus* 的三个组分，然后又鉴定了西部松小蠹 *Dendroctonus brevicomis* 的

聚集信息素的一个组分以及南部松小蠹 *D. frontalis* 聚集信息素的一个组分。由于聚集信息素在生产和环境保护中的巨大应用潜力，国外在这一领域的研究进展迅速，目前已从多种昆虫中分离并鉴定了聚集信息素，表 1 列出了部分已报道的昆虫聚集信息素的主要成分。

表 1 部分昆虫的聚集信息素
Table 1 Aggregation pheromones of some insects

种类 Species	聚集信息素成分 Components	来源 Source	参考文献 Reference
蜚螂目 Dictyoptera 德国小蠊 <i>Blattella germanica</i>	蜚螂亚目 Blattellide 1,1-二甲基胺-2-甲基-2-丙醇 1,1-dimethylamino-2-methyl-2-propanol; 氨 ammonia; 甲胺 methylamine; 二甲胺 dimethylamine; 三甲胺 trimethylamine 乳酸 lactic acid 1-(6 α -氯-4 β ,5 β -环氧-5 β -豆甾烷-3 β -基)- β -D-吡喃葡萄糖甙 1-(6 α -chloro-4 β ,5 β -epoxy-5 β -stigmast-3 β -yl)- β -D-glucopyranoside; 1-(6 α -氯-5-羟基-5 β -豆甾烷-3 β -基)- β -D-吡喃葡萄糖甙 1-(6 α -chloro-5 β -hydroxy-5 β -stigmast-3 β -yl)- β -D-glucopyranoside	♀、♂ 幼蠊 larva 成、幼蠊 adult and larva	Sakuma and Fukami, 1990 McFarland and Alli, 1986 Sakuma <i>et al.</i> , 1993
直翅目 Orthoptera 沙漠蝗 <i>Schistocerca gregaria</i>	蝗科 Acrididae 苯乙腈 phenylacetonitrile; 邻甲氧基苯酚 guaiacol; 苯酚 phenol 苯乙腈 phenylacetonitrile; 邻甲氧基苯酚 guaiacol; 苯酚 phenol; 茴香醚 anisole; 安息香醛 benzaldehyde; 藜芦醚 veratrole 安息香醛 benzaldehyde; 藜芦醚 veratrole; 苯乙腈 phenylacetonitrile; 4-乙基藜芦醚 4-ethylene veratrole 苯乙腈 phenylacetonitrile; 藜芦醚 veratrole	成、幼蝗 adult and larva ♂ 5 龄若虫 5th instar nymph 卵鞘泡沫 froth of egg pods	Obeng-Ofori <i>et al.</i> , 1994 Torto <i>et al.</i> , 1994 Assad <i>et al.</i> , 1997 Rai <i>et al.</i> , 1997
热带飞蝗 <i>Locusta migratoria</i>	苯乙腈 phenylacetonitrile; 邻甲氧基苯酚 guaiacol 和苯酚 phenol	成、幼蝗 adult and larva	Fuzeau-Braesch <i>et al.</i> , 1988
半翅目 Hemiptera 西针喙缘蝽 <i>Leptoglossus occidentalis</i>	缘蝽科 Coreidae 反-2-己烯醛(2E)-2-hexenal; 苯甲醇 benzyl alcohol; α -萜品醇 α -terpinenol; 里哪醇 linalool; 萜烯-4-醇 terpinen-4-ol; 顺-薄荷醇 cis-piperitol	♂	Blatt and Borden, 1996
褐珀蝽 <i>Plautia stali</i> Scott	蝽科 Pentatomidae 反-2,4-顺-6-三烯癸酸甲酯 methyl (E, E, Z)-2,4,6-decatrienolate	♂	Sugie <i>et al.</i> , 1996
桔刺蝽 <i>Biprorulus bibax</i> Breddin	(3R,4S,反1'-3,4-双丁基(1')四氢-2-呋喃醇(3R,4S,1'E)-3,4-bis(1'-butenyl)tetrahydro-2-furanol; 里哪醇 linalool; 法呢醇 farnesol; 橙花叔醇 nerolidol	♂	James <i>et al.</i> , 1994
<i>Pristhesancus plagipennis</i>	猎蝽科 Reduviidae 顺-3-己烯基-(R)-2-羟基-3-甲基丁酸(Z)-3-hexenyl-(R)-2-hydroxy-3-methylbutyrate; 3-甲基丁醇 3-methylbutanol; 2-苄基乙醇 2-phenylethanol; 顺-3-己烯-1-醇(3Z)-3-hexen-1-ol; 癸醛 decanal; 反-2-己烯酸(2E)-2-hexenoic acid	♂	James <i>et al.</i> , 1994
双翅目 Diptera <i>Drosophila busckii</i>	果蝇科 Drosophilidae (S)-2-十五烷基醋酸酯(S)-2-pentadecan-yl acetate; 2-十五碳酮 2-pentadecanone	♂	Schaner <i>et al.</i> , 1989
<i>D. buzzatii</i> <i>D. martensis</i> <i>D. serido</i>	顺-10-十七烯基-2-酮(10Z)-10-heptadecen-2-one	♂	Schaner and Jackson, 1992

续表 1

种类 Species	聚集信息素成分 Components	来源 Source	参考文献 Reference
<i>D. mulleri</i>	(S)-2-十三烷基醋酸酯(S)-2-tridecan-yl acetate; 反-10-十七烯基-2-酮 (10 <i>Z</i>)-10-heptadecen-2-one	♂	Bartelt <i>et al.</i> , 1989
	舌蝇科 Glossinidae		
刺舌蝇 <i>Glossina morsitans morsitans</i> W.	正十五烷 pentadecane	幼虫 larva	Saini <i>et al.</i> , 1996
<i>G. morsitans centralis</i> M.	正十二烷 dodecane	幼虫 larva	Saini <i>et al.</i> , 1996
鞘翅目 Coleoptera	长蠹科 Bostrychidae		
大粉长谷蠹 <i>Prostephanus truncatus</i>	1-甲基乙基(反 2)-2-乙基-2-戊烯酸酯 1-methylethyl (2 <i>E</i>)-2-methyl-2-pentenoate	♂	Cork <i>et al.</i> , 1991
<i>Rhyzopertha dominica</i>	(S)-(+) -1-甲基丁基(反 2)-2-甲基-2-戊烯酸酯(S)-(+) -1-methylbutyl(2 <i>E</i>)-2-methyl-2-pentenoate; (S)-(+) -1-甲基丁基(反 2)-2,4-二甲基-2-戊烯酸酯(S)-(+) -1-methylbutyl (2 <i>E</i>)-2,4-dimethyl-2-pentenoate	♂	Williams <i>et al.</i> , 1981
	扁甲科 Cucujidae		
锈赤扁谷盗 <i>Cryptolestes ferrugineus</i>	反-4,8-二甲基-4,8-癸二烯-10-交酯 (<i>E,E</i>)-4,8-dimethyl-4,8-decadien-10-olide; (顺 3,11 <i>S</i>)-3-十二碳烯-11-交酯(3 <i>Z</i> ,11 <i>S</i>)-3-dodecen-11-olide	♂	Wong <i>et al.</i> , 1983
长角扁谷盗 <i>C. pusillus</i>	顺-3-十二碳烯交酯(<i>Z</i>)-3-dodecenolide; 顺-5-十四碳烯基-13-交酯(<i>Z</i>)-5-tetradecen-13-olide; 顺-3,6-十二碳二烯交酯(<i>Z,Z</i>)-3,6-dodecadienolide	♂	Millar <i>et al.</i> , 1985
	象虫科 Curculionidae		
香蕉根象甲 <i>Cosmopolites sordidus</i>	(1 <i>S</i> ,3 <i>R</i> ,5 <i>R</i> ,7 <i>S</i>)-2,8-二-1-乙基-3,5,7-三甲基-二环[3.2.1]辛烷 (1 <i>S</i> ,3 <i>R</i> ,5 <i>R</i> ,7 <i>S</i>)-2,8-dioxa-1-ethyl-3,5,7-trimethyl-bicyclo[3.2.1]octane	♀、♂	Beauhaire <i>et al.</i> , 1995
<i>Dynamis borassi</i>	(<i>S,S</i>)-4-甲基-5-壬醇(4 <i>S</i> ,5 <i>S</i>)-4-methyl-5-nonanol	♂	Giblin <i>et al.</i> , 1997
西印度蔗象甲 <i>Metamasius hemipterus</i>	2-甲基-4-庚醇 2-methyl-4-heptanol; 4-甲基-5-壬醇 4-methyl-5-nonanol	♂	Cerda <i>et al.</i> , 1996
亚洲鼻隐喙象 <i>Rhynchophorus bilineatus</i>	(<i>S,S</i>)-4-甲基-5-壬醇(4 <i>S</i> ,5 <i>S</i>)-4-methyl-5-nonanol	♂	Oehlschlager <i>et al.</i> , 1995
<i>R. cruentatus</i>	5-甲基-4-辛醇 5-methyl-octan-4-ol	♂	Weissling <i>et al.</i> , 1994
椰棕象甲 <i>R. ferrugineus</i>	4-甲基-5-壬醇 4-methyl-5-nonanol 4-甲基-5-壬酮 4-methyl-5-nonanone	♂	Hallett <i>et al.</i> , 1993
棕榈象甲 <i>R. palmarum</i> L.	6-甲基-(反)-2-庚烯基-4-醇(2 <i>E</i>)-6-methyl-2-hepten-4-ol	♂	Rochat <i>et al.</i> , 1991
棕榈红隐喙象 <i>R. phoenicis</i>	3-甲基-4-辛醇 3-methyl-4-octanol	♂	Gries <i>et al.</i> , 1993
豌豆根瘤象 <i>Sitona lineatus</i> L.	4-甲基-3,5-戊二酮 4-methyl-3,5-heptanedione; 顺-3-己烯-1-醇(<i>Z</i>)-3-hexen-1-ol; 顺-3-己烯-1-乙酸酯(<i>Z</i>)-3-hexen-1-yl acetate; 里哪醇 linalool	♂	Blight <i>et al.</i> , 1984
	露尾甲科 Nitidulidae		
<i>Carpophilus antiquus</i>	3-甲基-5-乙基-反 2,4,6-壬三烯 (2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i>)-5-ethyl-3-methyl-2,4,6-nonatriene; 3,5-二甲基-7-乙基-反 2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>)-7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene; 4-甲基-6-乙基-反 3,5,7-癸三烯 decatriene (3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i>)-6-ethyl-4-methyl-3,5,7-decatriene	♂	Bartelt <i>et al.</i> , 1993

续表 1

种类 Species	聚集信息素成分 Components	来源 Source	参考文献 Reference
<i>C. brachypterus</i>	3,5,7-三甲基-反-2,4,6,8-癸四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 3,5,7-trimethyl-2,4,6,8-decatetraene; 3,5,7-三甲基-反-2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 3,5,7-trimethyl-2,4,6,8-undecatetraene; 3,5-二甲基-7-乙基-反-2,4,6,8-癸四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 7-ethyl-3,5-dimethyl-2,4,6,8-decatetraene; 4,6,8-三甲基-反-3,5,7,9-十一碳四烯(3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i> ,9 <i>E</i>) – 4,6,8-trimethyl-3,5,7,9-undecatetraene; 3,5-二甲基-7-乙基-反-2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene	♂	Willians <i>et al.</i> , 1995
<i>C. davidsoni</i>	3-甲基-5-乙基-反-2,4,6-壬三烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i>) – 5-ethyl-3-methyl-2,4,6-nonatriene; 4-甲基-6-乙基-反-3,5,7-癸三烯(3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i>) – 6-ethyl-4-methyl-3,5,7-decatriene; 3,5,7-三甲基-反-2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 3,5,7-trimethyl-2,4,6,8-undecatetraene; 3,5-二甲基-7-乙基-反-2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene	♂	Bartelt <i>et al.</i> , 1994
玉米露尾甲 <i>C. dimidiatus</i>	4-甲基-6,8-二乙基-反-3,5,7,9-十二碳四烯(3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i> ,9 <i>E</i>) – 6,8-diethyl-4-methyl-3,5,7,9-dodecatetraene; 9-甲基-5,7-二乙基-反-3,5,7,9-十三碳四烯(3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i> ,9 <i>E</i>) – 5,7-diethyl-9-methyl-3,5,7,9-tridecatetraene	♂	Bartelt <i>et al.</i> , 1995
酱曲露尾甲 <i>C. hemipterus</i>	3,5,7-三甲基-反-2,4,6,8-癸四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 3,5,7-trimethyl-2,4,6,8-decatetraene; 3,5,7-三甲基-反-2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 3,5,7-trimethyl-2,4,6,8-undecatetraene	♂	Bartelt <i>et al.</i> , 1990
玉米红褐露尾甲 <i>C. mutilatus</i>	3,5-二甲基-7-乙基-反-2,4,6,8-癸四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 7-ethyl-3,5-dimethyl-2,4,6,8-decatetraene; 3,5-二甲基-7-乙基-反-2,4,6,8-十一碳四烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i> ,8 <i>E</i>) – 7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene; 3-甲基-5-乙基-反-2,4,6-壬三烯(2 <i>E</i> ,4 <i>E</i> ,6 <i>E</i>) – 5-ethyl-3-methyl-2,4,6-nonatriene		Bartelt <i>et al.</i> , 1992
	7-甲基-5-乙基-反-3,5,7-十一碳三烯(3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i>) – 5-ethyl-7-methyl-3,5,7-undecatriene; 4-甲基-6-乙基-反-3,5,7-癸三烯(3 <i>E</i> ,5 <i>E</i> ,7 <i>E</i>) – 6-ethyl-4-methyl-3,5,7-decatriene	♂	Bartelt <i>et al.</i> , 1993
隐喙象科 Rhynchophoridae			
谷象 <i>Sitophilus granarius</i> L.	2 <i>S</i> -甲基-3 <i>R</i> -羟基戊酸-1-乙基丙酯(2 <i>S</i> ,3 <i>R</i>)-1-ethylpropyl-2-methyl-3-hydroxypentanoate	♂	Phillips <i>et al.</i> , 1987
米象 <i>S. oryzae</i> 玉米象 <i>S. zeamais</i>	5-羟基-4-甲基-3-戊酮 5-hydroxy-4-methyl-3-heptanone	♂	Phillips <i>et al.</i> , 1985
金龟子科 Scarabaeidae			
二疣独角仙 <i>Oryctes rhinoceros</i> L.	4-甲基辛酸 4-methyl octanoic acid; 4-甲基辛酸乙酯 ethyl 4-methyl-octanoate; 4-甲基庚酸乙酯 ethyl 4-methylheptanoate	♂	Hallett <i>et al.</i> , 1995
小蠹科 Scolytidae			
松圆头大小蠹 <i>Dendroctonus adjunctus</i>	瘤额大小蠹素 frontalin((<i>S</i> , <i>R</i>)-1,5-二甲基-6,8-二□-[3,2,1]-二环辛烷(1 <i>S</i> ,5 <i>R</i>)-1,5-dimethyl-6,8-dioxo-[3,2,1]-bicyclooctan); 顺-马鞭草烯醇 trans-verbenol; 外-西松大小蠹素 exo-brevicomín((1 <i>R</i>)-外-7-乙基-5-甲基-6,8-二□-二环[3.2.1]辛烷(1 <i>R</i>)-exo-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane)	♀、♂	Hughes <i>et al.</i> , 1986
西松大小蠹 <i>D. brevicomis</i>	西松大小蠹素 brevicomin	♀	Vite and Pitman, 1969

续表 1

种类 Species	聚集信息素成分 Components	来源 Source	参考文献 Reference
瘿额大小蠹 <i>D. frontalis</i>	西松大小蠹素 brevicomin; 瘿额大小蠹素 frontalin; 月桂烯 myrcene; 3-萜烯 3-carene	♀、♂	Pitman, 1969
	西松大小蠹素 brevicomin, 瘿额大小蠹素 frontalin, 马鞭草烯酮 verbenone, 松香芹酮 pinocarvone, 松香芹醇 pinocarveol, 顺-月桂烯醇 trans-myrtanol	♀、♂	Libbey <i>et al.</i> , 1974
	瘿额大小蠹素 frontalin; 顺-马鞭草烯醇 trans-verbenol	♂	Kinzer <i>et al.</i> , 1969
黄杉小蠹 <i>D. pseudotsugae</i>	马鞭草烯酮 verbenone	♀、♂	Rudinsky, 1973
	乙酸异戊酯 isoamyl acetate; 2-苯基乙醇 2-phenylethanol; 2-苯乙酸乙酯 2-phenylethyl acetate	♂	Brand <i>et al.</i> , 1977
	瘿额大小蠹素 frontalin; 黄杉小蠹烯醇 pseudenol(1-甲基环氧己-2-烯-1-醇 1-methylcyclohex-2-en-1-ol; 3-甲基环氧己-2-烯-1-醇 3-methyl cyclohex-2-en-1-ol); 乙醇 ethanol	♂	Pitman <i>et al.</i> , 1975
美云杉毛小蠹 <i>Dryocoetes affaber</i> M.	萜烯 terpenes	寄主 host	Pitman <i>et al.</i> , 1969
重齿小蠹 <i>Ips duplicatus</i>	(+)-外-西松大小蠹素(+)-exo-brevicomin; (+)-内-西松大小蠹素(+)-endo-brevicomin	♂	Camacho <i>et al.</i> , 1994
南部松齿小蠹 <i>I. grandicollis</i>	小蠹二烯醇 ipsdienol(2-甲基-6-亚甲基-2,7-辛二烯-4-醇 2-methyl-6-methylene-2,7-octadien-4-ol)	♂	Bakke, 1975
美东最小齿小蠹 <i>I. avulsus</i>	小蠹烯醇 ipsenol(2-甲基-6-亚甲基-7-辛烯-4-醇 2-methyl-6-methylene-7-octen-4-ol); 顺/反-马鞭草烯醇 cis/trans-verbenol	♂	Vite and Renwick, 1971
异加州齿小蠹 <i>I. paraconfusus</i>	(R)-(-)-小蠹二烯醇(R)-(-)-ipsdienol; (S)-(-)-小蠹烯醇(S)-(-)-ip-senol 顺/反-马鞭草烯醇 cis/trans-verbenol; 小蠹二烯醇 ipsdienol	♂	Vite <i>et al.</i> , 1978 Vite <i>et al.</i> , 1972
云杉松齿小蠹 <i>I. pini</i> S.	小蠹烯醇 ipsenol; 小蠹二烯醇 ipsdienol; 顺/反-马鞭草烯醇 cis/ trans-verbenol	♂	Vite <i>et al.</i> , 1972
云杉八齿小蠹 <i>I. typographus</i>	顺/反-马鞭草烯醇 cis/ trans-verbenol; 小蠹二烯醇 ipsdienol (2-羟基-4,4,6-三甲基-2,5-环己二烯-1-酮 2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one)	♂	Vite <i>et al.</i> , 1972 Teale <i>et al.</i> , 1991
中穴星坑小蠹 <i>P. chalcographus</i> L.	顺/反-马鞭草烯醇 cis/trans-verbenol; 小蠹二烯醇 ipsdienol; 小蠹烯醇 ipsenol	♂	Vite <i>et al.</i> , 1972 Bakke, 1977
<i>Pityokteines elegans</i>	2-甲基-3-丁基-2-醇 2-methyl-3-buten-2-ol	♂	
波纹棘胫小蠹 <i>Scolytus multistriatus</i>	2-乙基-1,6-二[4.4]螺壬烷 2-ethyl-1,6-dioxaspiro[4.4]nonane; (反 2,顺 4)-2,4-甲基癸二烯酸酯 methyl(2 <i>E</i> ,4 <i>Z</i>)-2,4-decadienoate; (-)-α/β-蒎烯(-)-α/β-pinene	♂	Francke <i>et al.</i> , 1977
<i>S. scolytus</i>	(S)-(-)-小蠹烯醇(S)-(-)-ipsenol; (+)-和(-)-小蠹二烯醇(+)-&(-)-ipsdienol; 小蠹烯酮 ipsenone	♂	Vite <i>et al.</i> , 1972
黑条木小蠹 <i>Trypodendron lineatum</i>	1-庚醇 heptan-1-ol; 波纹小蠹素 multistriatin(5-乙基-2,4-二甲基-6,8-二[3.2.1]辛烷 5-ethyl-2,4-dimethyl-6,8-dioxabicyclo[3.2.1]octane); 葑澄茄油烯 cubebene	♂	Cuthbert and Peacock, 1978
	4-甲基-3-庚醇 4-methyl-3-heptanone;	♂	Blight <i>et al.</i> , 1983
	己醛 hexanal; 1-己醇 hexan-1-ol	寄主 host	Dickens <i>et al.</i> , 1990
	4-甲基-3-庚醇 4-methyl-3-heptanone	♂	Blight <i>et al.</i> , 1983
黑条木小蠹 <i>Trypodendron lineatum</i>	苏-4-甲基-庚-3-醇 threo-4-methyl-heptan-3-ol; 庚-3-醇 heptan-3-ol; α-苏-4-甲基-波纹小蠹素 α-erythro-4-methyl-multistriatin	♂、♀	Blight <i>et al.</i> , 1978
	黑条木小蠹素 Lineatin((1 <i>R</i>)-1,3,3-三甲基-4,6-二[3.3.1.0 ^{2,7}]壬烷(1 <i>R</i>)-1,3,3-trimethyl-4,6-dioxatricyclo[3.3.1.0 ^{2,7}]nonane); 乙醇 ethanol; α-蒎烯 α-pinene	♂	Macconnell <i>et al.</i> , 1977

续表 1

种类 Species	聚集信息素成分 Components	来源 Source	参考文献 Reference
锯谷盗 <i>Oryzaephilus surinamensis</i> L.	锯谷盗科 <i>Silvanidae</i>		
	顺-3,6-十二碳二烯-11-交酯(3Z,6Z)-3,6-dodecadien-11-olide; 顺-3,6-十二碳二烯交酯(3Z,6Z)-dodecadienolide; 顺-5,8-十四碳二烯-13-交酯(5Z,8Z)-5,8-tetradecadien-13-olide	♂	Pierce <i>et al.</i> , 1985
隐翅虫 <i>Aleochara curtula</i>	隐翅虫科 <i>Staphylinidae</i>		
	顺-9-十六碳烯酸异丙酯 isopropenyl(Z9)-hexadecenoate	♂	Peschke <i>et al.</i> , 1999
黄粉虫 <i>Tenebrio molitor</i>	拟步行虫科 <i>Tenebrionidae</i>		
	乳酸 lactic acid	幼虫 larva	Weaver <i>et al.</i> , 1989
赤拟谷盗 <i>Tribolium castaneum</i>			
	4,8-二甲基癸醛 4,8-dimethyl decanal	♂	Suzuki and Mori, 1983
<i>T. freemani</i> H.	4,8-二甲基癸醛 4,8-dimethyl decanal	♂	Suzuki <i>et al.</i> , 1987

表 1 表明，目前所鉴定的昆虫聚集信息素主要是蜚蠊目、直翅目、半翅目、双翅目以及鞘翅目的昆虫所产生，而以鞘翅目昆虫为最多。昆虫聚集信息素的主要成分多为一些烃、醇、醛、酮、酯、酸、酸酐、胺以及腈类化合物，而且，多数昆虫的聚集信息素组分在同属中具有极大的相似性。

2 昆虫聚集信息素的来源及作用对象

昆虫聚集信息素与昆虫性信息素的区别之一是昆虫聚集信息素来源的多样化。雌雄成虫，若虫，幼虫均可以产生聚集信息素（见表 1），但在不同的类群中，来源和作用对象存在差异。多数种类的昆虫，雄虫可产生聚集信息素，通过腺体或排泄物释放，至少对两性成虫起作用。鞘翅目中，绝大多数种类的聚集信息素由雄虫产生，而对两性成虫均具有引诱能力。但蜚蠊目和直翅目中，一些种类不仅雄成虫/成螨可以释放聚集信息素，若虫/若螨也可以产生释放聚集信息素。沙漠蝗 *S. gregaria* 不仅成虫可以释放聚集信息素，而且 2~5 龄的若虫也释放聚集信息素，同时两者的成分完全不同（Assad *et al.*, 1997; Mahamat *et al.*, 1993）。在蜚蠊目中，成虫和若虫聚集信息素的一些组分相同，但乳酸由幼蠊产生，仅能引起幼蠊的聚集反应（McFarland and Alli, 1986）。而双翅目中，刺舌蝇和 *G. morsitans centralis* 各自的幼虫分别产生正十五烷和正十二烷，诱集妊娠雌虫产幼虫（Saini *et al.*, 1996）。

认为一些植物挥发性气味也是昆虫聚集信息素的观点引起定义上的争端。瘤额大小蠹、黄杉小蠹

烯醇和乙醇是黄杉小蠹 *D. pseudotsugae* 雌性产生的聚集信息素组分，符合信息素“同种性”条件，而萜烯由受害寄主产生，与前三种物质混合具有更强烈的引诱活性（Pitman *et al.*, 1975）。因此，把上述四种物质组成的混合物称为“黄杉小蠹聚集信息素”，虽然不符合聚集信息素严格的定义，但更能反映这些物质对黄杉小蠹聚集行为所起的作用，因为离开具体环境，昆虫信息素传递的信息可能失去意义。对多种小蠹，来自其自身、寄主或存在于环境中的萜烯类及其衍生物，以混合方式起作用能够提高种的特异性。表 1 中仅列出我们认为具代表性的波纹棘胫小蠹和黄杉小蠹。

目前的研究表明，一些昆虫的聚集信息素，专一性似乎不及其性信息素，表现在除了作用于同种的个体，还可对近源种起作用。如使用某些露尾甲的聚集信息素诱集露尾甲时，诱捕器中可诱到多种其它种类的露尾甲，尽管以该物质为聚集信息素的种类的诱捕数量最多（James *et al.*, 1996）。某种昆虫聚集信息素的某种主要成分，有时可以是同地近缘种的抗聚集信息素（anti-aggregation pheromone），如马鞭草烯酮既是云杉八齿小蠹（*I. typographus*）聚集信息素的主要组分（Vite *et al.*, 1972），同时又是黄杉小蠹 *D. pseudotsugae* 的抗聚集信息素（Ross and Daterman, 1997）。尽管云杉八齿小蠹与中穴星坑小蠹 *P. chalcographus* 的聚集信息素的成分完全相同（Vite *et al.*, 1972），二者却能有效避免相互之间的竞争（Byers, 1993），遗憾的是，其机制还很不清楚。有时，同一化学物质，在昆虫不同的阶段或状态所起作用不同：沙漠蝗 *S. gregaria* 5 龄若虫产生的聚集信息素，却抑制成

虫的性成熟 (Assad *et al.*, 1997); 雄成虫的聚集信息素, 促进年轻成虫的性成熟 (Mahamat *et al.*, 1993)。

一种昆虫的聚集信息素, 往往成为其天敌昆虫的利他素。运用大粉长谷蠹 *P. truncatus* 的聚集信息素诱集大粉长谷蠹, 能诱集到大量的大粉长谷蠹的一种捕食性天敌, 阎虫科的 *Teretriosoma nigrescens*, 进一步的电生理试验表明, *T. nigrescens* 对大粉长谷蠹的聚集信息素敏感 (Borgemeister *et al.*, 1997)。同样的现象也发生在一些小蠹及其天敌之间 (Francke *et al.*, 1995)。因此, 在利用昆虫聚集信息素进行害虫治理时, 如何更好地利用或保护天敌, 应当引起足够的重视。

3 影响昆虫聚集信息素效能的因子

昆虫聚集信息素受体的生理状态决定聚集信息素的效能。正十五烷和正十二烷分别是刺舌蝇和 *G. m. centralis* 产幼虫聚集信息素电生理活性最强的组分, 室内行为测定中, 两个组分明显吸引妊娠雌虫到产幼虫的地方, 但幼虫发育不充分时, 雌虫对该信息素不敏感, 产完幼虫后的雌虫, 对该信息素同样不敏感 (Saini *et al.*, 1996)。德国小蠊 *B. germanica* 独栖 5 龄若虫, 比群集个体对聚集信息素更敏感 (Rivault and Cloarec, 1998)。

对一些种类的昆虫, 寄主植物或食物的气味, 可能成为昆虫聚集信息素的增效剂。运用聚集信息素对多种露尾甲进行诱集时, 发酵的面团可以使诱捕效率显著提高 (James *et al.*, 1995)。同样, 发酵的甘蔗茎, 也能显著提高多种象甲聚集信息素对多种象甲的诱捕效率 (Giblin *et al.*, 1994)。

资源和环境的有效性, 同样可以影响昆虫聚集信息素的效能。室内试验表明, 相对湿度低于 70% 时, 产卵聚集信息素不能引起 *G. m. centralis* 妊娠雌虫的聚集 (Saini *et al.*, 1996)。其它生态因子如降雨量、气温等均可影响以聚集信息素作为诱饵的诱捕器对露尾甲或象甲的田间诱捕效果 (de Abreu, 1997; Bartelt *et al.*, 1994; Hallett *et al.*, 1999)。

4 昆虫聚集信息素的应用

昆虫聚集信息素主要应用于虫情监测和害虫的可持续治理。

以昆虫聚集信息素作为诱捕器的诱饵, 定期检查诱捕的害虫数量, 从而为害虫的治理提供依据。最初, 昆虫聚集信息素应用于森林害虫小蠹的防治, 后来, 又在露尾甲上成功应用 (James *et al.*, 1995)。对于某些仓储害虫, 如谷象, 还可以用聚集信息素辅助研究其分布 (Plarre, 1996)。

应用昆虫聚集信息素能有效对害虫进行可持续治理。聚集信息素与杀虫剂混用, 诱杀半翅目害虫以及一些鞘翅目害虫 (Ross and Daterman, 1997)。昆虫聚集信息素可通过以下途径增效: 添加一些植物性增效剂 (Bartelt *et al.*, 1995); 添加死虫或活虫 (Bartelt *et al.*, 1995); 结合使用模拟的寄主 (El Garhy, 1996)。在应用昆虫聚集信息素进行害虫防治时, 应用“诱集—驱避”策略, 更可以得到显著的效果, 如在需要保护的植物或地带使用抗聚集信息素 (anti-aggregation pheromone) 或其它驱避剂, 而在次要植物或次要地带使用聚集信息素 (Ross and Niwa, 1997)。

5 有聚集行为而尚未鉴定出聚集信息素组分的昆虫

尽管科技进步使昆虫聚集信息素的成分鉴定越来越容易, 但昆虫聚集信息素的化学结构鉴定与生物活性鉴定毕竟是需要耐心的工作。迄今已有多种昆虫被发现具有聚集习性, 尤其是鳞翅目、同翅目和脉翅目的一些昆虫有聚集习性 (见表 2)。然而, 到目前为止, 多种有聚集习性的昆虫, 仍未鉴定出其聚集信息素。

6 结论

昆虫聚集信息素在有害生物可持续治理中的潜在价值, 推动了昆虫聚集信息素的研究。三十多年来, 多种昆虫的聚集信息素已被鉴定, 一些昆虫聚集信息素的生物合成、昆虫对聚集信息素的行为反应以及昆虫聚集信息素的应用均取得了一定的进展。但是, 人类目前对昆虫聚集信息素的认知仍然有限, 而且, 昆虫的聚集行为并非仅由其聚集信息素调节, 实际上, 利他素、性信息素以及报警信息素等其它一些信息化学物质诱导的聚集行为已引起人们的注意。对于有聚集行为的昆虫, 必须研究清楚为何聚集, 何时聚集, 怎样聚集等基本问题, 否则将限制信息化学物质在有害生物可持续治理中的

常规应用。从现在看，引起昆虫聚集行为的信息化学物质的种类固然重要，而更急待解决的是从效应角度严格对这些物质做定量分析：估计信息化学物

质的纯度；定量分析这些物质的释放速率；采用标准化指标描述昆虫生理状态；定量分析气味感受的临界点；详尽探讨不同环境中的行为反应。

表 2 有聚集行为而尚未鉴定出聚集信息素组分的昆虫

Table 2 Insects with aggregation behavior but their aggregation pheromones still unknown

类群	种 类
半翅目 Hemiptera	牧草盲蝽 <i>Lygus lineolaris</i> (McLaughlin <i>et al.</i> , 1998), 条蜂缘蝽 <i>Riptortus linearis</i> (Higuchi and Nakamori, 1999), 侵扰锥猎蝽 <i>Triatoma infestans</i> (Lorenzo and Lazzari, 1996), 海壁蝽 <i>Piezodorus hybneri</i> G. (Higuchi, 1999), <i>T. mazzottii</i> , <i>T. longipennis</i> , <i>T. barberi</i> (Cruz <i>et al.</i> , 1995)
直翅目 Orthoptera	<i>Dociostaurus maroccanus</i> (Arias <i>et al.</i> , 1994)
鞘翅目 Coleoptera	松树皮象 <i>Hylobius abietis</i> L. (Zagatti <i>et al.</i> , 1997), <i>Maladera matrida</i> Argaman (Harari <i>et al.</i> , 1994)
双翅目 Diptera	<i>Rhagoletis tomatis</i> (Frias, 1995), <i>Lutzomyia longipalpis</i> (Kelly and Dye, 1997), 辣椒果实蝇 <i>Bactrocera latifrons</i> (Jackson and Long, 1997)
鳞翅目 Lepidoptera	<i>Conipia hector</i> Butler (Sone, 1995)
同翅目 Homoptera	草莓谷网蚜 <i>Sitobion fragariae</i> , 禾谷缢管蚜 <i>Rhopalosiphum padi</i> (Hardie <i>et al.</i> , 1996)
脉翅目 Neuroptera	<i>Euroleon nostras</i> (Yasseri <i>et al.</i> , 1997)

参 考 文 献 (References)

Aldrich J R, Blum M S, Lloyd H A, Fales H M, 1978. Pentatomid natural products. Chemistry and morphology of the III-IV dorsal abdominal glands of adults. *J. Chem. Ecol.*, 4, : 161-172.

Arias A, Sanchez M, Jimenez J, 1994. Soil distribution of eggs pods of *Dociostaurus maroccanus* (Thunb.) and importance of predation in two farms in Extremadura. *Boletin de Sanidad Vegetal, Plagas*, 20: (1): 3-22.

Assad Y O H, Hassanali A, Torto B, Mahamat H, Bashir N H H, El Bashir S, 1997. Effects of fifth-instar volatiles on sexual maturation of adult desert locust *Schistocerca gregaria*. *J. Chem. Ecol.*, 23 (5): 1 373-1 388.

Bakke A, 1975. Aggregation pheromone in the bark beetle *Ips duplicatus* (Sahlberg). *Norw. J. Ent.*, 22: 67-69.

Bakke A, 1977. Field response to a new pheromonal compound isolated from *Ips typographus*. *Naturwissenschaften*, 64: 98.

Bartelt R J, Vetter R S, Carlson D G, Baker T C, 1994. Responses to aggregation pheromones for five *Carpophilus* species (Coleoptera: Nitidulidae) in a California date garden. *Environmental Entomology*, 23 (6): 1 534-1 543.

Bartelt R J, Vetter R S, Carlson D G, Petroski R J, Baker T C, 1995. Pheromone combination lures for *Carpophilus* (Coleoptera: Nitidulidae) species. *Journal of Economic Entomology*, 88 (4): 864-869.

Bartelt R J, James D G, 1994. Aggregation pheromone of Australian sap be-

etle, *Carpophilus davidsoni* (Coleoptera: Nitidulidae). *J. Chem. Ecol.*, 20: 3 207-3 219.

Bartelt R J, Carlson D G, Vetter R S, Baker T C, 1993. Male-produced aggregation pheromone of *Carpophilus mutilatus* (Coleoptera: Nitidulidae). *J. Chem. Ecol.*, 19: 107-118.

Bartelt R J, Weaver D K, Arbogast R T, 1995. Aggregation pheromone of *Carpophilus dimidiatus* (F.) (Coleoptera: Nitidulidae) and responses to *Carpophilus* pheromones in South Carolina. *J. Chem. Ecol.*, 21: 1 763-1 779.

Bartelt R J, Weisleder D, Dowd P F, Plattner R D, 1992. Male-specific tetraene and triene hydrocarbons of *Carpophilus hemipterus*: structure and pheromonal activity. *J. Chem. Ecol.*, 18: 379-402.

Bartelt R J, Seaton K L, Dowd P F, 1993. Aggregation pheromone of *Carpophilus antiquus* (Coleoptera: Nitidulidae) and kairomonal use of *C. lugubris* pheromone by *C. antiquus*. *J. Chem. Ecol.*, 19: 2 203-2 216.

Bartelt R J, Dowd P F, Plattner R D, Weisleder D, 1990. Aggregation pheromone of driedfruit beetle, *Carpophilus hemipterus*. Wind-tunnel bioassay and identification of two novel tetraene hydrocarbones. *J. Chem. Ecol.*, 16: 1 015-1 039.

Bartelt R J, Schaner A M, Jackson L L, 1989. Aggregation pheromone components in *Drosophila mulleri*. A chiral ester and an unsaturated ketone. *J. Chem. Ecol.*, 15: 399-411.

Beauhaire J, Ducrot P-H, Malosse C, Rochat D, Ndiege I O, Otieno D O, 1995. Identification and synthesis of sordidin, a male pheromone emitted by *Cosmopolites sordidus*. *Tetrahedron Letters*, 36: 1 043-1 046.

- Blatt S E, Borden J H, 1996. Evidence for a male produced aggregation pheromone in the western conifer seed bug, *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae). *The Canadian Entomologist*, 128: 777–778.
- Blight M M, Pickett J A, Smith M C, Wadhams L J, 1984. An aggregation pheromone of *Sitona lineatus*. *Naturwissenschaften*, 71: 480.
- Blight M M, Wadhams L J, Wenham M J, 1978. Volatiles associated with unmated *Scolytus scolytus* beetles on english elm: differential production of α -multistriatin and 4-methyl-3-heptanol, and their activities in a laboratory bioassay. *Insect Biochem.*, 8: 135–142.
- Blight M M, Henderson N C, Wadhams L J, 1983. The identification of 4-methyl-3-heptanone from *Scolytus scolytus* (F.) and *S. multistriatus* (Marsham). Absolute configuration, laboratory bioassay and electrophysiological studies on *S. scolytus*. *Insect Biochem.*, 13: 27–38.
- Borgemeister C, Djossou F, Adda C, Schneider H, Djomamou B, Degbey P, Azoma B, Markham R H, 1997. Establishment, spread, and impact of *Tetrestoma nigrescens* (Coleoptera: Histeridae), an exotic predator of the larger grain borer (Coleoptera: Bostrichidae) in southwestern Benin. *Environmental Entomology*, 26 (6): 1 405–1 415.
- Brand J M, Schultz J, Barras S J, Edson L J, Payne T L, Hedden R L, 1977. Bark-beetle pheromones. Enhancement of *Dendroctonus frontalis* (Coleoptera: Scolytidae) aggregation pheromone by yeast metabolites in laboratory bioassay. *J. Chem. Ecol.*, 3: 657–666.
- Byers J A, 1993. Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. *Experientia*, 49 (3): 272–275.
- Camacho A D, Pierce H D Jr, Borden J H, 1994. Aggregation pheromones in *Dryocoetes affaber* (Mann.) (Coleoptera: Scolytidae): stereoisomerism and species specificity. *J. Chem. Ecol.*, 20: 111–124.
- Cerda H, Fernandez G, Lopez A, Vargas J, 1996. Study of *Metamasius hemipterus* (Coleoptera: Curculionidae) attraction to host plant odours and aggregation pheromones. *Cana de Azucar.*, 14 (2): 53–70.
- Cork A, Hall D H, Hodges R J, Pickett J A, 1991. Identification of major component of male-produced aggregation pheromone of larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). *J. Chem. Ecol.*, 17: 789–803.
- Cruz L L, Malo E A, Rojas J C, 1995. Aggregation pheromone in five species of Triatominae (Hemiptera: Reduviidae). *Memorias do Instituto Oswaldo Cruz.*, 90 (5): 645–648.
- Cuthbert R A, Peacock J W, 1978. Response of the elm bark beetle, *Scolytus multistriatus* (Coleoptera: Scolytidae), to component mixtures and doses of the pheromone, multilure. *J. Chem. Ecol.*, 4: 363–373.
- de Abreu J M, 1997. Attraction of *Carpophilus dimidiatus* and *C. obsoletus* (Coleoptera: Nitidulidae) to aggregation pheromones in stored cocoa. *Agrotropica*, 9 (2): 41–48.
- Dickens J C, Jang E B, Light D M, Alford A R, 1990. Enhancement of insect pheromone responses by green leaf volatiles. *Naturwissenschaften*, 77: 29–31.
- Du J W, 1988. Pheromone of insects and their application. Beijing: Forestry Publishing Company of China. [杜家纬, 1988. 昆虫信息素及其应用. 北京, 中国林业出版社]
- Du J W, 1991. Our progress in the pheromone of insects. *Bulletin of the Chinese Academy of Sciences*, 6 (4): 326–328. [杜家纬, 1991. 我们在昆虫信息素方面的研究进展. 中国科学院院刊, 6 (4): 326–328]
- El Garhy M E, 1996. Field evaluation of the aggregation pheromone of the red palm weevil, *Rhynchophorus ferrugineus*, in Egypt. Brighton Crop Protection Conference: Pests and Diseases–1996. Vol. 3. British Crop Protection Council, Farnham, UK. 1 059–1 064.
- Francke W, Bartels J, Meyer H, Schroder F, Kohnle U, Baader E, Vite J P, 1995. Semiochemicals from bark beetles: new results, remarks, and reflections. *J. Chem. Ecol.*, 21 (7): 1 043–1 063.
- Francke W, Heemann V, Gerken B, Renwick J A A, Vite J P, 1977. 2-Ethyl-1, 6-dioxaspiro [4.4] nonane, principal aggregation pheromone of *Pityogenes chalcographus* (L.). *Naturwissenschaften*, 64: 590–591.
- Frias L D, 1995. Oviposition behaviour of *Rhagoletis tomatitis* on tomato (*Lycopersicum esculentum*) (Diptera: Tephritidae). *Acta Entomologica Chilena*, 19: 159–162.
- Fuzeau-Braesch S, Genin E, Jullien R, Knowles E, Papin C, 1988. Composition and role of volatile substances in atmosphere surrounding two gregarious locusts, *Locusta migratoria* and *Schistocerca gregaria*. *J. Chem. Ecol.*, 14: 1 023–1 033.
- Giblin Davis R M, Gries R, Gries G *et al.*, 1997. Aggregation pheromone of palm weevil, *Dynamis borassi*. *J. Chem. Ecol.*, 23 (10): 2 287–2 297.
- Giblin Davis R M, Weissling T J, Oehlschlager A C, Gonzalez L M, 1994. Field response of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae) to its aggregation pheromone and fermenting plant volatiles. *Florida Entomologist*, 77 (1): 164–177.
- Gries G, Gries R, Perez A L, Oehlschlager A C, Gonzales L M, Poerce H D Jr, Kouda Bonafos M, Zebeyou M, Nanou N, 1993. Aggregation pheromone of the African palm weevil, *Rhynchophorus phoenicis* F. *Naturwissenschaften*, 80: 90–91.
- Hallett R H, Oehlschlager A C, Borden J H, 1999. Pheromone-trapping protocols for the Asian palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *International Journal of Pest Management*, 45 (3): 231–237.
- Hallett R H, Perez A L, Gries G, Gries R, Pierce H D Jr, Yue J, Oehlschlager A C, Gonzalez L M, Borden J H, 1995. Aggregation pheromone of coconut rhinoceros beetle, *Oryctes rhinoceros* (L.) (Coleoptera: Scarabaeidae). *J. Chem. Ecol.*, 21: 1 549–1 570.
- Hallett R H, Gries G, Gries R, Borden J H, Oehlschlager A C, Pierce H D Jr, Angerilli N P D, Rauf A, 1993. Aggregation pheromones of two Asian palm weevils, *Rhynchophorus ferrugineus* and *R. vulneratus*. *Naturwissenschaften*, 80: 328–331.
- Harari A R, Ben Yakir D, Rosen D, 1994. Mechanism of aggregation behavior in *Maladera matrida* Argaman (Coleoptera: Scarabaeidae). *J. Chem. Ecol.*, 20 (2): 361–371.
- Hardie J, Storer J R, Cook F J, 1996. Sex pheromone and visual trap interactions in mate location strategies and aggregation by host alternating aphids in the field. *Physiological Entomology*, 21 (2): 97–106.
- Higuchi H, Nakamori H, 1999. Attraction of conspecific adults and nymphs by adults of *Riptortus linearis* (Fabricius) (Heteroptera: Alydidae).

- Applied Entomology and Zoology*, 34 (4): 455–458.
- Higuchi H, 1999. Attraction of conspecific individuals by adults of *Piezodorus hybneri* (Gneline) (Heteroptera: Pentatomidae). *Japanese Journal of Applied Entomology and Zoology*, 43 (4): 205–206.
- Hughes P R, Renwick J A A, Vite J P, 1976. The identification and field bioassay of chemical attractants in the roundheaded pine beetle. *Environ. Entomol.*, 5: 1 165–1 168.
- Jackson C G, Long J P, 1997. Mating behaviour of *Bactrocera latifrons* (Diptera: Tephritidae) in field cages. *Annals of the Entomological Society of America*, 90 (6): 856–860.
- James D G, Bartelt R J, Moore C J, 1996. Mass trapping of *Carpophilus* spp. (Coleoptera: Nitidulidae) in stone fruit orchards using synthetic aggregation pheromones and a contractant: development of a strategy for population suppression. *J. Chem. Ecol.*, 22 (8): 1 541–1 556.
- James D G, Faulder R J, Bartelt R J, 1995. Fauna and seasonal abundance of *Carpophilus* spp. (Coleoptera: Nitidulidae) in four stone fruit growing regions of southeastern Australia as determined by pheromone-trapping. *Journal of the Australian Entomological Society*, 34 (4): 327–333.
- James D G, Moore C J, Aldrich J R, 1994. Identification, synthesis, and bioactivity of a male-produced aggregation pheromone in assassin bug, *Pristhesancus plagipennis* (Hemiptera: Reduviidae). *J. Chem. Ecol.*, 20: 3 281–3 295.
- James D G, Mori K, Aldrich J R *et al.*, 1994. Flight-mediated attraction of *Biprorulus bibax* Breddin (Hemiptera: Pentatomidae) to natural and synthetic aggregation pheromone. *J. Chem. Ecol.*, 20: 71–80.
- Kelly D W, Dye C, 1997. Pheromones, kairomones and aggregation dynamics of the sandfly *Lutzomyia longipalpis*. *Animal Behaviour*, 53 (4): 721–731.
- Kinzer G W, Fentiman A F, Page T F, Folt R L, Vite J P, Pitman G B, 1969. Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. *Nature*, 221: 477–478.
- Libbey L M, Morgan M E, Putnam T B, Rudinsky J A, 1974. Pheromones released during inter- and intra-sex response of the scolytid beetle *Dendroctonus brevicornis*. *J. Insect Physiol.*, 20: 1 667–1 671.
- Liu M Y, 1994. A study on the pheromone in insects and its new advance in application. *Entomological Knowledge*, 31 (1): 56–59. [刘孟英, 1994. 昆虫信息素研究及应用的新进展. *昆虫知识*, 31 (1): 56–59]
- Lorenzo M G, Lazzari C R, 1996. The spatial pattern of defaecation in *Triatoma infestans* and the role of faeces as a chemical mark of the refuge. *J. Insect Physiol.*, 42 (9): 903–907.
- Macconnell J G, Borden J H, Silverstein R M, Stokkink E, 1977. Isolation and tentative identification of lineatin, a pheromone from the frass of *Trypodendron lineatum* (Coleoptera: Scolytidae). *J. Chem. Ecol.*, 3: 549–561.
- Mahamat H, Hassanali A, Odongo H, Torto B, El Bashir E S, 1993. Studies on the maturation accelerating pheromone of the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae). *Chemoecology*, 4: 159–164.
- McFarland J E, Alli I, 1986. Aggregation of larvae of *Blattella germanica* (L.) by lactic acid present in excreta. *J. Chem. Ecol.*, 12 (6): 1 369–1 376.
- McLaughlin J R, Dugger P, Richter D, 1998. The status of *Lygus* pheromone research. 1998 Proceedings Beltwide Cotton Conferences, San Diego, California, USA, 5–9 January 1998. Volume 2. 938–940. National Cotton Council, Memphis, USA
- Millar J G, Pierce H D Jr, Pierce A M, Oehlschlager A C, Borden J H, Barak A V, 1985. Aggregation pheromones of the flat grain beetle, *Cryptolestes pusillus* (Coleoptera: Cucujidae). *J. Chem. Ecol.*, 11: 1 053–1 070.
- Obeng-Ofori D, Torto B, Njagin P G N, Hassanali A, Amiani H, 1994. Fecal volatiles as part of the aggregation pheromone complex of the desert locust, *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae). *J. Chem. Ecol.*, 20: 2 077–2 087.
- Oehlschlager A C, Prior R N B, Perez A L, Gries R, Gries G, Pierce H D Jr, Laup S, 1995. Structure, chirality, and field testing of a male-produced aggregation pheromone of Asian palm weevil *Rhynchophorus bilineatus* (Montr.) (Coleoptera: Curculionidae). *J. Chem. Ecol.*, 21: 1 619–1 629.
- Peschke K, Friedrich P, Kaiser U, Franke S, Franke W, 1999. Isopropyl (29)-hexadecenoate as a male attractant pheromone from the sternal gland of the rove beetle *Aleochara curtula* (Coleoptera: Staphylinidae). *Chemoecology*, 9 (2): 47–54.
- Phillips J K, Walgenbach C A, Klein J A, Burkholder W E, Schuff N R P, Fales H M, 1985. (R*, S*)-5-Hydroxy-4-methyl-3-heptanone. Male-produced aggregation pheromone of *Sitophilus oryzae* (L.) and *S. zeamais* Motsch. *J. Chem. Ecol.*, 11: 1 263–1 274.
- Phillips J K, Miller S P F, Andersen J F, Fales H M, Burkholder W E, 1987. The chemical identification of the granary weevil aggregation pheromone. *Tetrahedron Letters*, 28: 6 145–6 146.
- Pierce A M, Pierce H D Jr, Oehlschlager A C, Borden H H, 1985. Macrolide aggregation pheromones in *Oryzaephilus surinamensis* and *Oryzaephilus mercator* (Coleoptera: Cucujidae). *J. Agric. Food Chem.*, 33: 848–852.
- Pitman G B, 1969. Pheromone response in pine bark beetles: influence of host volatiles. *Science*, 166: 905–906.
- Pitman G B, Hedden R L, Gara R I, 1975. Synergistic effects of ethyl alcohol on the aggregation of *Dendroctonus pseudotsugae* (Col., Scolytidae) in response to pheromones. *Z. ang. Ent.*, 78: 203–208.
- Plarre R, 1996. Three dimensional distribution of *Sitophilus granarius* (L.) (Coleoptera: Curculionidae) in wheat influenced by the synthetic aggregation pheromone. *J. Stor. Prod. Res.*, 32 (3): 275–283.
- Rai M M, Hassanali A, Saini R K, Odongo H, Kahoro H, 1997. Identification of components of the oviposition aggregation pheromone of the gregarious desert locust, *Schistocerca gregaria* (Forsk.). *J. Insect Physiol.*, 43 (1): 83–87.
- Rivault C, Cloarec A, 1998. Cockroach aggregation: discrimination between strain odours in *Blattella germanica*. *Animal Behaviour*, 55 (1): 177–184.
- Rochat D, Malosse C, Lettere M, Ducrot P–H, Zagatti P, Renou M, Descoins C, 1991. Male-produced aggregation pheromone of the American palm weevil, *Rhynchophorus palmarum* (L.) (Coleoptera, Curculionidae).

- idae): collection, identification, electrophysiological activity, and laboratory bioassay. *J. Chem. Ecol.*, 17: 2 127–2 141.
- Ross D W, Daterman G E, 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas fir beetle. *Forest Science*, 43 (1): 65–70.
- Ross D W, Niwa C G, 1997. Using aggregation and antiaggregation pheromones of the Douglas-fir beetle to produce snags for wildlife habitat. *Western Journal of Applied Forestry*, 12 (2): 52–54.
- Rudinsky J A, 1973. Multiple functions of the southern pine beetle pheromone verbenone. *Environ. Entomol.*, 2: 511–514.
- Saini R K, Hassanali A, Andoke J, Ahuya P, Ouma W P, 1996. Identification of major components of larviposition pheromone from larvae of tsetse flies *Glossina morsitans morsitans* Westwood and *Glossina morsitans centralis* Machado. *J. Chem. Ecol.*, 22 (7): 1 211–1 220.
- Sakuma M, Fukami H, 1993. Aggregation arrestant pheromone of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): isolation and structure elucidation of blastellastanoside-A and -B. *J. Chem. Ecol.*, 19: 2 521–2 541.
- Sakuma M, Fukami H, 1990. The aggregation pheromone of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): isolation and identification of the attractant components of the pheromone. *Appl. Ent. Zool.*, 25: 355–368.
- Schaner A M, Jackson L L, 1992. (Z)-10-Heptadecen-2-one and other 2-ketones in the aggregation pheromone blend of *Drosophila martensis*, *D. buzzatii*, and *D. sordo*. *J. Chem. Ecol.*, 18: 53–64.
- Schaner A M, Tanico-Hogan L D, Jackson L L, 1989. (S)-2-pentadecyl acetate and 2-pentadecanone. Components of aggregation pheromone of *Drosophila busckii*. *J. Chem. Ecol.*, 15: 2 577–2 588.
- Sone K, 1995. Insecticide application effects on the emergence of the glassy wings *Conipia hector* (B.) (Lepidoptera: Aegeriidae). *Memoris of the Faculty of Agriculture, Kagoshima University*, 31: 53–61.
- Sugie H, Yoshida M, Kawasaki K, Noguchi H, Moriya S, Takagi K, Fukuda H, Fujiie A, Yamanaka M, Ohira Y, Tsutsumi T, Tsuda K, Fukumoto K, Yamashita M, Suzuki H, 1996. Identification of the aggregation pheromone of the brown-winged green bug, *Plautia stali* Scott (Heteroptera: Pentatomidae). *Appl. Ent. Zool.*, 31: 427–431.
- Suzuki T, Mori K, 1983. (4R, 8R)-(-)-4,8-dimethyldecanal: the natural aggregation pheromone of the red flour beetle, *Tribolium castaneum* (Coleoptera: Tenebrionidae). *Appl. Ent. Zool.*, 18: 134–136.
- Suzuki T, Nakakita H, Kuwahara Y, 1987. Aggregation pheromone of *Tribolium freemani* Hinton (Coleoptera: Tenebrionidae) I. Identification of aggregation pheromone. *Appl. Ent. Zool.*, 22: 340–347.
- Teale S A, Webster F X, Zhang A, Lanier G N, 1991. Lanierone: a new pheromone component from *Ips pini* (Coleoptera: Scolytidae) in New York. *J. Chem. Ecol.*, 17: 1 159–1 176.
- Torto B, Njagi P G N, Hassanali A, Amiani H, 1994. Aggregation pheromone system of adult gregarious desert locust *Schistocerca gregaria* (Forsk.). *J. Chem. Ecol.*, 20: 1 749–1 762.
- Vite J P, Pitman G B, 1969. Insect and host odors in the aggregation of the western pine beetle. *Can. Ent.*, 101: 113–117.
- Vite J P, Renwick J A A, 1971. Population aggregating pheromone in the bark beetle, *Ips grandicollis*. *J. Insect Physiol.*, 17: 1 699–1 704.
- Vite J P, Bakke A, Renwick J A A, 1972. Pheromones in *Ips* (Coleoptera: Scolytidae): occurrence and production. *Can. Ent.*, 104: 1 967–1 975.
- Vite J P, Ohloff G, Billings R F, 1978. Pheromonal chirality and integrity of aggregation response in southern species of the bark beetle *Ips* sp. *Nature*, 272: 817–818.
- Weaver D K, McFarlane J E, Alli I, 1989. Aggregation in yellow mealworms, *Tenebrio molitor* L. (Coleoptera: Tenebrionidae) larvae. I. Individual and group attraction to frass and isolation of an aggregant. *J. Chem. Ecol.*, 15: 1 605–1 615.
- Weissling T J, Giblin-Davis R M, Gries G, Gries R, Perez A L, Pierce H D Jr, Oehlschlager A C, 1994. Aggregation pheromone of palmetto weevil, *Rhynchophorus cruentatus* (F.) (Coleoptera: Curculionidae). *J. Chem. Ecol.*, 20: 505–515.
- Williams H J, Silverstein R M, Burkholder W E *et al.*, 1981. Dominicalure 1 and 2: components of aggregation pheromone from male lesser grain borer *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae). *J. Chem. Ecol.*, 7: 759–784.
- Williams R N, Ellis M S, Bartelt R J, Khorramshahi A, 1995. Efficacy of *Carpophilus* aggregation pheromones on nine species in northeastern Ohio, and identification of the pheromone of *C. brachypterus*. *Ent. Exp. Appl.*, 77 (2): 141–147.
- Wong J W, Verigin V, Oehlschlager A C, Borden J H, Pierce H D Jr, Pierce A M, Chong L, 1983. Isolation and identification of two macrocyclic pheromones from the frass of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae). *J. Chem. Ecol.*, 9: 451–474.
- Zagatti P, Lemperiere G, Malosse C, 1997. Monoterpenes emitted by the large pine weevil, *Hyllobius abietis* (L.) feeding on Scots pine, *Pinus sylvestris* L. *Physiological Entomology*, 22 (4): 394–400.